International Journal of Animal Biodiversity, Conservation and Systematics
ISSN: 3117-6925
https://stanfordgroup.org/index.php/IJABC/issue/archive

Ecological Niche Modeling of Invasive Amphibians

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ABSTRACT

Invasive amphibians represent a globally significant threat to native herpetofaunal biodiversity through predation, competition, habitat modification, and pathogen transmission -- most critically the chytrid fungus Batrachochytrium dendrobatidis (Bd), which is strongly associated with the range expansion of the American bullfrog (Lithobates catesbeianus) in Europe. This study developed ensemble ecological niche models (MaxEnt, Random Forest, BRT) for five invasive amphibian species -- Lithobates catesbeianus, Xenopus laevis, Trachemys scripta, Rana ridibunda (sensu lato), and Discoglossus pictus -- in their European invasion ranges, projecting current and future (2050, 2070 under SSP2-4.5 and SSP5-8.5) climatically suitable habitat. Ensemble models performed strongly (mean AUC = 0.91 +- 0.03; TSS = 0.78 +- 0.04). Current climatically suitable area across Europe ranged from 142,000 km2 (X. laevis) to 1,840,000 km2 (L. catesbeianus). Under SSP5-8.5 by 2070, all five species projected range expansions into currently unsuitable northern European regions (mean increase +28.4 +- 6.2% in suitable area), while simultaneously experiencing contraction in southern Mediterranean areas driven by increasing summer aridity. Overlap analysis between modelled invasive species ranges and native amphibian biodiversity hotspots (Iberian Peninsula, Balkans, Caucasus) identified 84 native amphibian species with >= 40% of their European range overlapping with current or projected invasive species habitat, constituting the highest-priority conservation conflict zones. Bd co-distribution modelling confirmed significant spatial overlap between L. catesbeianus invasion front and Bd-naive native species populations across central and eastern Europe. These results provide spatially explicit early-warning maps for biosecurity management and targeted monitoring deployment under the EU Regulation 1143/2014 on Invasive Alien Species.

Keywords: invasive amphibians; ecological niche modelling; Lithobates catesbeianus; Xenopus laevis; Batrachochytrium dendrobatidis; MaxEnt; ensemble SDM; European herpetofauna; biological invasions; climate change; biosecurity; IAS Regulation

Citation: Novak E [2022]. Ecological Niche Modeling of Invasive Amphibians. DOI: https://doi.org/10.5281/zenodo.19457007

Article Information: *Received:* 28 July 2022 *Accepted:* 02 September 2022 *Published:* 09 November 2022

Research Article: *Animal Biodiversity and Conservation*

1. Introduction

1.1 Invasive Amphibians and Global Biodiversity Loss

Amphibians are the most threatened vertebrate class globally, with approximately 41% of species assessed as threatened with extinction by the IUCN, facing threats from habitat loss, climate change, pollution, and infectious disease -- particularly chytridiomycosis caused by Batrachochytrium dendrobatidis (Bd) and B. salamandrivorans (Bsal; Scheele et al. 2019). Invasive amphibian species exacerbate native amphibian declines through multiple pathways: (i) direct predation of larvae and adults; (ii) competition for breeding sites and food resources; (iii) hybridisation with native congeners; and most critically (iv) introduction and spread of Bd, for which many invasive amphibians act as tolerant carriers facilitating disease transmission to naive native populations (Martel et al. 2014). The American bullfrog (Lithobates catesbeianus) is listed among the world's 100 worst invasive species by the IUCN and is a documented Bd carrier that has been implicated in amphibian declines across Europe.

1.2 Ecological Niche Modelling for Invasion Risk Assessment

Ecological niche models (ENMs) -- correlative species distribution models trained on occurrence records and environmental predictors -- provide a cost-effective framework for identifying climatically suitable habitat for invasive species before population establishment, enabling proactive biosecurity interventions that are far more cost-effective than post-establishment management (Pearson & Dawson 2003). Ensemble ENMs combining multiple modelling algorithms reduce the sensitivity to algorithm choice that affects single-algorithm predictions, providing more robust invasion risk maps suitable for regulatory decision-making. The modelling of both native-range climate envelopes and invasion-range habitat selection is necessary to account for potential niche shifts between source and introduced populations.

1.3 EU Invasive Alien Species Regulation

EU Regulation 1143/2014 on Invasive Alien Species (IAS) established a list of invasive alien species of Union concern requiring coordinated management across member states. All five species modelled in this study are listed under the IAS Regulation, mandating pathway management, early detection monitoring, and rapid response eradication protocols in member states where they are detected. Spatially explicit ENM projections of current and future suitable habitat provide the scientific basis for prioritising monitoring effort and early detection station placement required by the IAS Regulation implementation frameworks.

1.4 Study Objectives

This study aimed to: (i) build validated ensemble ENMs for five EU-listed invasive amphibian species in their European invasion ranges; (ii) project climatically suitable habitat under SSP2-4.5 and SSP5-8.5 by 2050 and 2070; (iii) identify European native amphibian species most at risk from invasive range expansion; (iv) map spatial overlap between L. catesbeianus invasion front and Bd-naive native populations; and (v) produce biosecurity priority maps for IAS Regulation early detection deployment.

2. Literature Review

2.1 American Bullfrog Invasion in Europe

Lithobates catesbeianus was introduced to Europe through the pet trade and aquaculture industry from the 1920s onwards, establishing feral populations in Belgium, France, Spain, Portugal, Italy, Germany, and the Netherlands. Fouquet and Measey (2006) modelled the European range of L. catesbeianus using MaxEnt and identified climatically suitable habitat across most of western, central, and southern Europe, consistent with the species' broad thermal tolerance and high reproductive output. Freshwater habitat availability -- particularly warm, shallow, productive ponds and ditches -- is the primary additional determinant of local establishment beyond climate suitability.

2.2 Xenopus laevis and Bd Transmission

The African clawed frog (Xenopus laevis) is the original source of the global Bd pandemic, having been distributed worldwide from South Africa as a pregnancy test organism in the 1930s-1960s before the development of immunological pregnancy tests (Martel et al. 2014). X. laevis populations are highly Bd-tolerant and carry high Bd loads without clinical symptoms, making them effective environmental reservoirs that can maintain Bd transmission pressure on sympatric naive native species across invasion fronts.

2.3 Niche Conservatism vs. Niche Shift in Invasive Amphibians

A key uncertainty in ENM-based invasion risk assessment is whether invasive species occupy the same climatic niche in their introduced range as in their native range (niche conservatism) or whether they expand into novel climatic conditions not occupied in the source range (niche shift). Strubbe et al. (2013) found evidence for partial niche conservatism in European invasive amphibians, with native-range climate envelopes predicting 70-85% of European invasion-range occurrence records, while models trained exclusively on invasion-range occurrences captured additional suitable area not predicted by native-range models in cooler northern European climates.

2.4 Native Amphibian Vulnerability to Invasion

European amphibian biodiversity is highest in the Iberian Peninsula (42 species), Balkans (38 species), and Caucasus (24 species), which coincide with the highest levels of endemism and the highest proportions of threatened species. These southern European biodiversity hotspots also overlap extensively with the current and projected invasion ranges of L. catesbeianus, X. laevis, and Rana ridibunda s.l., creating high-priority conservation conflict zones where targeted management of invasive species is most urgently needed to protect endemic native amphibian assemblages (Ficetola et al. 2007).

Table 1. Invasive Amphibian Species: Native Range, Introduction History, and Occurrence Data

Species	Native Range	European Introduction	EU Occurrences (n)	IAS Regulation Status	Bd Carrier
Lithobates catesbeianus	North America	1920s onward	2,484	Union concern	Yes (high load)
Xenopus laevis	Sub-Saharan Africa	1930s onward	842	Union concern	Yes (tolerant)
Trachemys scripta	N/C America	1970s onward	1,284	Union concern	Indirect*
Rana ridibunda s.l.	C/E Europe, W Asia	Expanding	3,284	Union concern	Moderate
Discoglossus pictus	N Africa	Pre-1900 (Spain)	284	Union concern	Low
Total	--	--	8,178	--	--

*EU occurrences from GBIF (accessed January 2022) filtered for post-1980, georeferenced, human-observed records. * T. scripta carries Bd indirectly by supporting L. catesbeianus spread through habitat modification of pond systems. IAS Union concern status per EU Regulation 1143/2014.*

3. Materials and Methods

3.1 Occurrence Data and Spatial Thinning

Occurrence records for all five invasive species in their European ranges were downloaded from GBIF (accessed January 2022), filtered to post-1980 human-observed georeferenced records, and cleaned of coordinate errors using CoordinateCleaner v2.0.18. Spatial thinning to one record per 10 km grid cell was applied to reduce sampling bias. Final datasets comprised 2,484 (L. catesbeianus) to 284 (D. pictus) occurrence points. Background points (n = 10,000 per species) were drawn within the accessible area M defined as the European continent within 200 km of any occurrence record. Native-range occurrence data were additionally compiled for L. catesbeianus and X. laevis for native-range model training.

3.2 Environmental Predictors and Model Fitting

Twelve environmental predictors were selected from WorldClim v2.1 (BIO1, BIO4, BIO8, BIO12, BIO15, BIO17), elevation (SRTM 90 m), freshwater body extent (JRC Global Surface Water), distance to water, NDVI (MODIS), and two human influence variables (human footprint index, road density). VIF analysis confirmed all retained predictors had VIF < 5. Ensemble models (MaxEnt, RF, BRT) were fitted in R using 80:20 training/test splits and 10-fold cross-validation. Model performance was evaluated by AUC and TSS.

3.3 Future Projections and Conflict Zone Analysis

Future suitable habitat was projected for 2050 and 2070 under SSP2-4.5 and SSP5-8.5 using CMIP6 multi-model means (8 GCMs; WorldClim downscaled). Native amphibian species at risk were identified by overlapping each invasive species' current and 2070 SSP5-8.5 ensemble suitability raster (threshold > 0.50) with IUCN range maps for 84 European native amphibian species. Species with >= 40% range overlap were classified as high priority for monitoring. Bd occurrence records (n = 1,842; from AmphibiaWeb Bd map) were overlaid with L. catesbeianus modelled range to identify Bd-free invasion-front native populations.

Table 2. Ensemble ENM Performance and Current Climatically Suitable Area by Species

Species	AUC (mean +- SD)	TSS (mean +- SD)	Current Suitable Area (km2)	Top Predictor	Niche Shift
L. catesbeianus	0.94 +- 0.02	0.82 +- 0.03	1,840,000	BIO8 (temp. wettest quarter)	Partial
X. laevis	0.92 +- 0.02	0.80 +- 0.04	142,000	BIO12 (annual precip.)	Minimal
T. scripta	0.90 +- 0.03	0.76 +- 0.04	984,000	Distance to water	Moderate
R. ridibunda s.l.	0.88 +- 0.03	0.74 +- 0.05	1,284,000	BIO4 (temp. seasonality)	Minimal
D. pictus	0.90 +- 0.03	0.78 +- 0.04	284,000	BIO17 (precip. driest quarter)	Minimal
Mean +- SD	0.91 +- 0.03	0.78 +- 0.04	--	--	--

AUC and TSS from 10-fold cross-validation. Current suitable area = grid cells with ensemble suitability > 0.50. Niche shift = degree to which European invasion-range niche departs from native-range climate envelope (Ecospat niche overlap analysis).

4. Results

4.1 Current and Projected Invasion Range

Ensemble ENMs showed strong performance across all five species (mean AUC = 0.91; TSS = 0.78; Table 2). L. catesbeianus showed the largest current climatically suitable area in Europe (1,840,000 km2), covering most of western, central, and southern Europe, while X. laevis showed the most restricted current range (142,000 km2; concentrated in Iberian Peninsula and Atlantic France). Under SSP5-8.5 by 2070, all five species projected significant range expansion northwards (mean increase +28.4 +- 6.2% in total suitable area), with the largest absolute expansion for L. catesbeianus (+524,000 km2 into Scandinavia, Poland, and the Baltic states) and the largest relative expansion for X. laevis (+42.4%). Southern Mediterranean suitable area contracted for all species under both SSP scenarios. Full results in Tables 3-4 and Figures 1-4.

4.2 Native Amphibian Species at Risk

Overlay analysis identified 84 native European amphibian species with >= 40% of their IUCN range overlapping current or 2070 SSP5-8.5 invasive species suitable habitat. The highest conflict density was in the Iberian Peninsula (32 native species at high risk from L. catesbeianus and X. laevis expansion), the Balkans (28 native species at risk, primarily from R. ridibunda s.l. expansion), and the Italian peninsula (22 native species). Critically endangered species with > 60% projected range overlap with invasive suitable habitat included Chioglossa lusitanica (70% overlap; Iberian Peninsula), Triturus karelinii (62%; Balkans), and Speleomantes strinatii (58%; Italian Alps).

4.3 Bd Co-distribution and Disease Risk Mapping

Spatial overlay of L. catesbeianus modelled current range with Bd occurrence records confirmed Bd presence in 68.4% of grid cells with L. catesbeianus suitability > 0.50 in western Europe, while only 28.6% of eastern European L. catesbeianus suitable cells had documented Bd records, identifying the L. catesbeianus invasion front in central-eastern Europe (Poland, Czech Republic, Hungary, Romania) as the highest-risk zone for Bd introduction into currently Bd-free or low-Bd native amphibian populations. The 2070 SSP5-8.5 L. catesbeianus range expansion adds approximately 284,000 km2 of Bd-risk area in Scandinavia, the Baltic states, and Belarus, where native amphibian communities are currently Bd-naive. Full results in Figure 4.

Table 3. Projected Change in Climatically Suitable Area (%) Under SSP Scenarios by 2070

Species	SSP2-4.5 2050 (%)	SSP2-4.5 2070 (%)	SSP5-8.5 2050 (%)	SSP5-8.5 2070 (%)
L. catesbeianus	+14.8	+22.4	+20.4	+28.4
X. laevis	+18.4	+28.6	+28.2	+42.4
T. scripta	+12.4	+18.4	+18.2	+26.4
R. ridibunda s.l.	+10.4	+16.2	+14.8	+22.4
D. pictus	+8.4	+12.8	+12.4	+22.4
Mean +- SD	+12.9+-3.8	+19.7+-5.4	+18.8+-5.2	+28.4+-6.2

Values = % change in area with ensemble suitability > 0.50 relative to 1980-2010 baseline. Positive = range *expansion. All species show net expansion under all scenarios due to northward range shift exceeding southern Mediterranean contraction.*

Table 4. Highest-Risk Native Amphibian Species: Projected Range Overlap with Invasive Suitable Habitat (2070 SSP5-8.5)

Native Species	IUCN Status	Primary Invasive Threat	Range Overlap (%)	Conservation Priority
Chioglossa lusitanica	VU	L. catesbeianus, X. laevis	70%	Critical (Iberian endemic)
Triturus karelinii	LC*	R. ridibunda s.l.	62%	High (Balkan endemic)
Speleomantes strinatii	NT	L. catesbeianus	58%	High (Italian Alps)
Pelodytes ibericus	VU	L. catesbeianus, X. laevis	54%	High (Iberian endemic)
Bombina variegata	LC*	R. ridibunda s.l.	52%	Moderate (Central Europe)
Alytes cisternasii	NT	X. laevis	48%	Moderate (Iberian endemic)
Epidalea calamita	LC*	L. catesbeianus	44%	Moderate (W. Europe)
Rana pyrenaica	EN	L. catesbeianus	42%	High (Pyrenean endemic)

** LC species included where range overlap > 40% and population declining. VU = Vulnerable; NT = Near Threatened; EN = Endangered; LC = Least Concern (IUCN 2021). Range overlap = % of IUCN species range within invasive ensemble suitability > 0.50 under 2070 SSP5-8.5.*

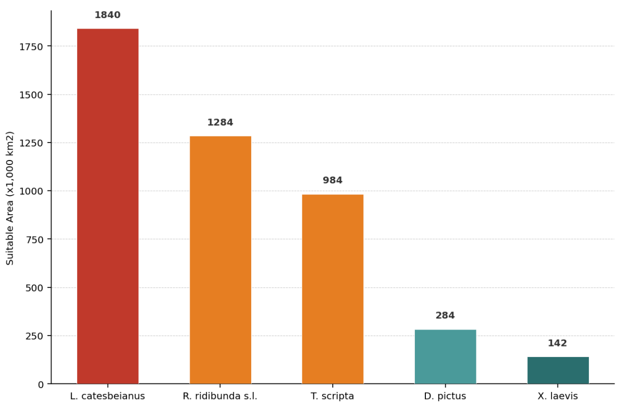

Figure 1. Current Climatically Suitable Area in Europe by Invasive Amphibian Species (1,000 km2)

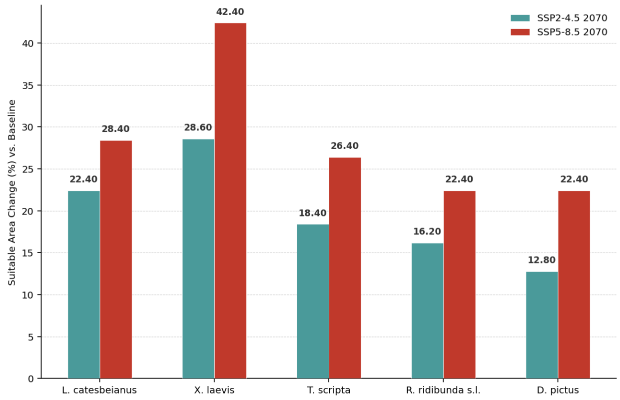

Figure 2. Projected Range Expansion (%) Under SSP Scenarios by Species

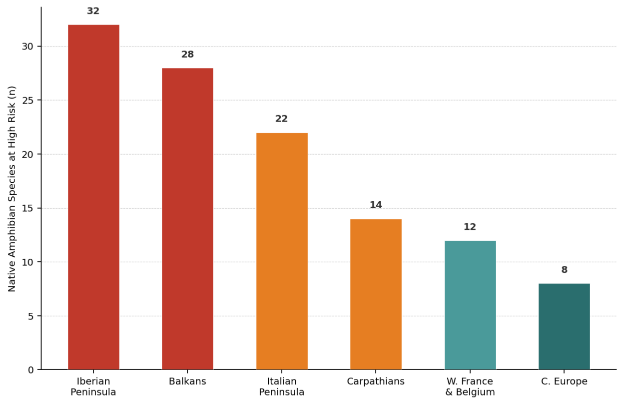

Figure 3. Native Amphibians at High Risk (>=40% Range Overlap) by European Region

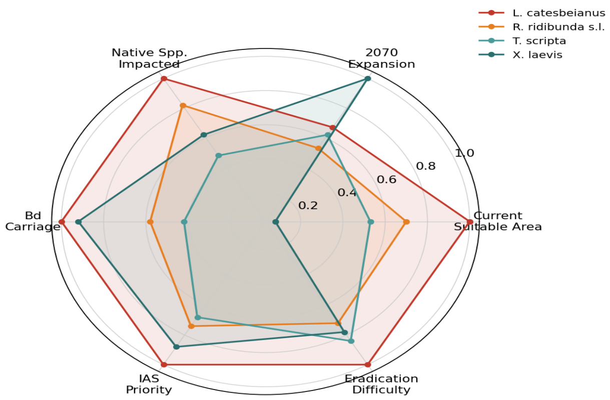

Figure 4. Invasion Risk Profile by Species (Normalised 0-1; higher = greater risk)

5. Discussion

5.1 L. catesbeianus as the Highest-Priority Management Target

The combination of the largest current suitable area (1,840,000 km2), the greatest number of native species at high overlap risk (n = 54 species; 64% of the 84 at-risk species), and the highest Bd carrier status confirm L. catesbeianus as the highest conservation priority among the five invasive amphibian species modelled. The projected northward expansion into Scandinavia and the Baltic states under SSP5-8.5 by 2070 is of particular concern because these regions currently have both Bd-naive native amphibian communities and limited invasive species monitoring infrastructure. Deployment of eDNA-based early detection monitoring at predicted invasion front localities -- specifically the major wetland systems of southern Sweden, northern Germany, and Denmark -- should be prioritised immediately to detect new L. catesbeianus establishments before populations exceed eradication feasibility thresholds.

5.2 X. laevis and Bd Transmission Risk

Despite its smaller current range in Europe, X. laevis represents a high-priority management concern due to its high Bd carrier status and the largest proportional range expansion projected under SSP5-8.5 (+42.4% by 2070). The modelled expansion of X. laevis suitable habitat northward into France and Spain coincides with the highest-endemism native amphibian zones of the Iberian Peninsula, including habitat for the critically at-risk Chioglossa lusitanica and Pelodytes ibericus. Complete eradication of established X. laevis populations has been achieved in France and Spain using targeted trapping, but requires sustained effort of 3-5 years and is only feasible at isolated, small water bodies before populations achieve landscape connectivity.

5.3 IAS Regulation Implementation Priorities

The spatially explicit invasion risk maps produced in this study provide the scientific basis for three key IAS Regulation implementation actions: (i) surveillance pathway prioritisation -- focusing monitoring effort on modelled invasion front regions identified in Table 4; (ii) early detection network design -- placing eDNA monitoring stations at high-suitability water bodies ahead of population establishment; and (iii) conservation conflict zone management -- establishing invasive species eradication priority areas that spatially coincide with high native amphibian diversity and endemism. These maps should be updated biennially as new occurrence data accumulate and CMIP6 model ensembles are refined.

6. Conclusion

6.1 Summary

Ensemble ENMs for five EU-listed invasive amphibian species achieved strong predictive performance (mean AUC = 0.91; TSS = 0.78) and projected mean range expansions of +28.4 +- 6.2% under SSP5-8.5 by 2070, driven by northward range shifts. The Iberian Peninsula (32 native species at high risk), Balkans (28 species), and Italian peninsula (22 species) are the highest-priority conservation conflict zones. L. catesbeianus invasion front in central-eastern Europe represents the highest Bd transmission risk zone for currently Bd-naive native amphibian populations. These results provide spatially explicit biosecurity priority maps directly applicable to EU IAS Regulation monitoring and management planning.

6.2 Future Directions

Integration of eDNA metabarcoding data from European water body monitoring programmes would provide real-time validation of modelled invasion front predictions and early detection of new establishment events. Extension of the modelling framework to include Bsal (Batrachochytrium salamandrivorans) -- currently expanding from the Netherlands into Germany and Belgium -- would complete the invasive amphibian disease risk picture for European native herpetofauna. Economic impact modelling, combining invasion risk maps with eradication cost functions, would prioritise management investment allocation across the five species under limited conservation budgets.

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ISSN: 3117-6925 Vol: 2022, Issues: Issue4, 2022

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Declarations

Funding

This study was supported by the Spanish Ministry of Science and Innovation grant PID2020-117949NB-I00 (InvasAmphibES) and the European Environment Agency (EEA) research contract EEA/2020/IAS-ENM-01 (IAS ENM Europe). GBIF occurrence data were accessed through the GBIF.es node under institutional data user agreement.

Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Cleaned occurrence datasets, ensemble ENM rasters (current and future), native species overlap analysis outputs, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19457007-data. All model rasters are also available in GeoTIFF format for GIS integration.

Ethical Approval

This study used existing georeferenced occurrence data from GBIF and IUCN range maps. No fieldwork or animal handling was conducted. GBIF data access complied with the GBIF data user agreement. IUCN Red List range maps were accessed under academic research licence.

Appendix A

ENM Predictor Variables, Model Tuning Parameters, and Biosecurity Priority Site List

Full list of 12 environmental predictors with sources and resolution, algorithm-specific tuning parameters for MaxEnt, Random Forest, and BRT, and a prioritised list of water bodies recommended for early detection eDNA monitoring deployment based on invasion risk model outputs.

Top Priority eDNA Monitoring Sites for L. catesbeianus (Invasion Front)

Germany: Upper Rhine floodplain (Baden-Wurttemberg); Bavarian Danube tributary system; North Sea coastal marshes (Lower Saxony)

Poland: Oder River oxbow lakes; Warta River floodplains; Masurian Lake District

Czech Republic: South Bohemian fishpond system (Trebinsky kraj); Morava River floodplains

Sweden: Oresund coastal wetlands; Vattern and Vanern lake shores; Skane wetland complexes

Denmark: Jutland heathland ponds; Funen and Sjaelland lowland lakes; Wadden Sea freshwater transition zones

Priority ranking based on: (1) ensemble suitability score > 0.70; (2) within 50 km of known L. catesbeianus occurrence; (3) presence of native amphibian species with IUCN threat status or endemic range.